

Effects of high- vs. low-yield environments on selection for increased biomass yield in switchgrass

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Received: 9 January 2007 / Accepted: 20 February 2007 / Published online: 14 March 2007
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Abstract No information is available on the effects of different biomass yield environments on selection efficiency in switchgrass (*Panicum virgatum* L.) breeding improvement. This study was conducted to assess the effects of high- and low-biomass yield environments (HYE and LYE, respectively) on recurrent selection for general combining ability (RSGCA) in a lowland population of switchgrass (NL-94). The top 14 of 65 NL-94 C₀ parent plants were selected based on biomass yield of half-sib (HS) progeny tested for one post-establishment year under HYE and LYE conditions. Nine of the 14 C₀ parent plants were the same based on HS performance under HYE and LYE. Selected plants were intercrossed to produce NL-94 HYE and NL-94 LYE C₁

populations. One hundred and twenty-five HS C₁ progeny families (60 NL-94 HYE and 65 NL-94 LYE) were evaluated for biomass yield for 3 years (2002–2004) under HYE and LYE conditions. The HYE produced about 2.5 times higher biomass yields than the LYE in both C₀ and C₁ HS progeny tests. Estimated additive genetic variance and predicted gains from selection (ΔG) were high in the C₁ populations indicating that RSGCA should achieve higher biomass yields. Mean biomass yields of C₁ HS families originating from the LYE protocol were significantly higher than those of families originating from the HYE protocol in both HYE and LYE performance tests, suggesting greater selection response under LYE in the C₀ population. The estimates of narrow-sense heritability (h_n^2) and ΔG from the C₁ populations indicate that positive response to selection for biomass yield is possible in subsequent cycles of selection under either HYE or LYE, with a possible small advantage for HYE.

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Keywords Biomass yield · Genetic gain ·
Heritability · Recurrent selection · Selection
environment · Switchgrass

Abbreviations

HS	Half-sib
HYE	High-yield environment
LYE	Low-yield environment

RSGCA Recurrent selection for general combining ability

Introduction

Switchgrass (*Panicum virgatum* L.) is a warm-season, perennial species indigenous to the North American tall grass prairies east of the Rocky Mountains (Hopkins et al. 1995). It is a highly outcrossed and genetically heterogeneous bunchgrass that assimilates carbon via the C₄ photosynthetic pathway (Sanderson 1992). Traditional uses for switchgrass are as livestock herbage and soil stabilization. In the early 1990s switchgrass was chosen by the US Department of Energy through its Biomass Feedstock Development Program as a model species on which to focus research aimed at developing a herbaceous energy crop (HEC) (McLaughlin et al. 1999). Switchgrass was chosen because of its broad geographic adaptation, ability to grow on marginal soils, and high biomass production capability with minimal inputs (McLaughlin et al. 1999).

The strategy to develop switchgrass as a HEC crop includes breeding to develop cultivars with enhanced biomass yield capability. The breeding method commonly used to improve quantitatively inherited traits (such as biomass yield) in populations of outcrossing species such as switchgrass is recurrent selection for general combining ability (RSGCA) (Poehlman & Sleper 1995). Banziger and Cooper (2001) noted that selection response for any given trait in the target environment is greatest when high levels exist for each of four factors, namely, genetic variance, selection intensity, heritability in the selection environment, and genetic correlation between selection and target environments. They noted that the genetic correlation between trait performance in the selection (low-input systems for tropical maize by CIMMYT) and target environments (highly variable low-input rainfed farming systems in Australia) derives from the relationship between the expression of genes controlling trait variation in the environments where the

germplasm is selected and deployed, respectively. Accordingly, it is important to know if germplasm accessions rank similarly in the selection and target environments. Betran et al. (2003) found that grain yield differences between maize (*Zea mays* L.) inbred lines and hybrids increased with the intensity of drought stress, but found significant interactions for combining abilities of inbred lines due to differences in soil nitrogen (N). They noted that the type of gene action appeared to be different under drought and low N, with additive effects more important under drought and dominance effects more important under low N.

Results from studies on the effects of variable yield environment on selection and cultivar performance vary from crop to crop. Gotoh and Osania (1959) reported that selection for increased grain yield in wheat (*Triticum aestivum* L.) was more effective under a low-yield environment (LYE) than under a high-yield environment (HYE). Conversely, Allen et al. (1978) found that selection for grain yield in soybean and wheat was more effective under HYE than under LYE. Vela-Cardenas and Frey (1972) reported equal effectiveness in selection for seed weight in oat (*Avena sativa* L.) under HYE and LYE. Whitehead and Allen (1990) concluded that low-stress environments commonly used in breeding soybean (*Glycine max* L.) should provide high probabilities for selecting superior lines for performance in both low- and high-stress edaphic conditions.

Little information is available on the response of switchgrass to selection for increased biomass production. A successful switchgrass cultivar used as a HEC would likely be grown on marginal soils with minimal fertility inputs. Cultivars developed from HYE may not perform well when grown in LYE and vice versa. Thus, it is important to know if the yield environment under which breeding is conducted affects the performance level and stability of derived cultivars.

The objectives of this study were to evaluate and compare the effectiveness of selection conducted in HYE and LYE on improving a C₀ switchgrass lowland population for biomass yield potential and to determine and compare genetic parameters in the resulting C₁ populations.

Materials and methods

Population formation and experimental design

To test the effects of HYE and LYE on plant selection, clonal sets of half-sib (HS) progeny were grown in two environments. In 1996, HS seed were collected from 65 randomly selected, spaced (1.1 m) plants from a 925 plant lowland switchgrass population designated as 'NL-94'. The NL-94 population resulted from two cycles of restricted recurrent phenotypic selection (RRPS) for biomass yield within the variety 'Kanlow' at a selection intensity of approximately 20%. The RRPS procedures used were those described by Burton (1982). For the purposes of this study the NL-94 population is considered the initial C_0 generation used for recurrent selection based on HS progeny evaluation. Eight HS plants were grown in the greenhouse from seed harvested from each of the 65 randomly selected parents. Four clonal plants were then produced from each of the 520 HS plants. Those plants were used to establish HYE and LYE yield tests in spring 1997 at Stillwater, OK (36.16°N Latitude, 97.09°W Longitude) on Oklahoma Agricultural Experiment Station sites approximately 2 km apart. A randomized complete block design (RCBD) with two replications was used for both tests. Each HS plant was clonally replicated two times in each experiment. Greenhouse grown plants were transplanted to the field on 1.1 m centers. A row of plants, not harvested for biomass yield data, was planted around each test to guard against border effects. The soils for the HYE and LYE were a Kirkland silt loam (fine, mixed, superactive, thermic Udertic Paleustolls) and a less productive Huska silt loam (fine, mixed, superactive, thermic Mollic Natrustalfs), respectively. The HYE test received annual early spring applications of 90 kg N ha⁻¹ plus P and K as indicated by soil test recommendations. The HYE test was irrigated during the growing season as needed to maintain good growing conditions. The LYE test received no fertilizer or supplemental water. Surflan[®] herbicide (oryzalin: 3,5-dinitro-*N*4, *N*4-dipropylsulfanilamide) was applied to both tests annually in early spring at the rate of 2.24 kg ha⁻¹ a.i. to prevent volunteer

switchgrass establishment and control weeds. Dry biomass yields of HS progeny plants were measured in 1998, 1999, and 2000 near the end of the growing seasons. The HYE and LYE progeny biomass yield data from 1998 were respectively used to choose the top 14 of the 65 original selected plants in the NL-94 nursery as parents. Biomass yield data from the HYE and LYE HS tests were also collected in 1999 and 2000 to determine if there were differences in selection of parent plants based on one (1998) vs. three (1998–2000) mean HS yield performance. The C_0 generation was grown under HYE conditions.

Parent plants selected on the basis of HS performance were intercrossed in 1999 (14 × 14 Latin square design, one block, field isolation) to produce new cyclic populations designated as NL-94 HYE C_1 and NL-94 LYE C_1 . The NL-94 HYE C_1 and NL-94 LYE C_1 selection nurseries, each comprising 1,020 plants (1.1 m spacing, 12 × 85 rows/columns), were established in early spring 2000. For this study, HS seed was collected by hand stripping from 200 randomly chosen plants within the respective nurseries in fall 2000. Seed from the individual plants was processed to near 100% purity and planted in rows (one row/plant) in greenhouse flats containing a standard soil mix. Not all of the 200 plants in the respective nurseries produced adequate clean seed and seed of some plants exhibited poor germination. In spring 2001, 125 HS progeny families (60 from the NL-94 HYE C_1 and 65 from the NL-94 LYE C_1) were planted in HYE and LYE tests at Stillwater, OK. The 60 and 65 HS families were respectively assigned to groups designated S_{HYE} or S_{LYE} (selection under high- and low-yield environment protocols, respectively, hereafter termed S_{HYE} and S_{LYE} protocols). The HYE test was on a relatively fertile Port silt loam soil (fine-silty, mixed, superactive, thermic Cumulic Haplustolls) while the LYE test was on the same site, Huska silt loam (fine, mixed, superactive, thermic Mollic Natrustalfs) and under the same conditions as described for the C_0 HS families. The HYE test received the same cultural practices as previously described. A RCBD with four replications was used for both tests. Plant spacing was 1.06 m. An individual plot consisted of three HS plants. Individual plants of the two HS trials were

harvested in the fall of 2002, 2003, and 2004. Individual plants were harvested with a one-row, tractor-mounted flail chopper. Aliquot samples from plants were dried at approximately 50°C for 5–7 days to determine dry matter (dm) concentration which was used in converting plant wet weights to a dm basis.

Statistical procedures

Data were analyzed in each year and over years for the respective test environments and the combined environments using ordinary least squares in the PROC MIXED (REML) procedure of SAS (SAS Institute 1999). For the combined analysis, the data were arranged as a split plot in space and time. A four-factor analysis of variance was performed on HS plot mean data collected for all environments and years using the following statistical model:

$$Y_{ijklm} = \mu + \alpha_i + \beta_{j(i)} + \tau_k + \gamma_{l(k)} + \delta_m + \alpha\tau_{ik} \\ + \alpha\delta_{im} + \beta\tau_{jk(i)} + \beta\delta_{jm(i)} + \tau\delta_{km} + \alpha\tau\delta_{ikm} \\ + \beta\tau\delta_{jkm(i)} + e_{n(ijklm)}$$

where μ is overall mean of biomass yield, α_i is fixed effect of protocol i , $\beta_{j(i)}$ is random effect of family (genotype) j within protocol i , τ_k is fixed effect of environment k , $\gamma_{l(k)}$ is random effect of replication l within environment k , δ_m is fixed effect of year m , $\alpha\tau_{ik}$ is fixed interaction effect of protocol i and environment k , $\alpha\delta_{im}$ is fixed interaction effect of protocol i and year m , $\beta\tau_{jk(i)}$ is random interaction effect of family j and environment k within protocol i , $\beta\delta_{jm(i)}$ is random interaction effect of family j and year m within protocol i , $\tau\delta_{km}$ is fixed interaction effect of environment k and year m , $\alpha\tau\delta_{ikm}$ is fixed interaction effect of protocol i , environment k , and year m , $\beta\tau\delta_{jkm(i)}$ is random interaction effect of

family j , environment k , and year m within protocol i , and $e_{n(ijklm)}$ is experimental error, mean 0, variance σ^2 .

Analyses were also conducted within selection protocols, environments, and group–environment combinations in order to obtain estimates of h_n^2 and ΔG for comparative purposes. For these analyses, the corresponding terms were omitted from the statistical model.

Examination of genotype-by-environment (GE) interaction was also accomplished via Spearman's rank correlation in the PROC CORR procedure in order to determine rank similarity between families in HYE and LYE (SAS Institute 1999).

Because of significant disparity between variances associated with the HYE and LYE environments as determined via F -test ($P < 0.01$), the data were transformed via square roots for all analyses conducted over environments.

Estimates of h_n^2 were obtained via a variance component method as described by Nguyen and Sleper (1983). The variance component method based on the analysis of variance procedures provides the greatest flexibility for predicting the effectiveness of alternative selection procedures (Fehr 1987). Estimates of h_n^2 were obtained on an individual plant basis and a phenotypic family mean (PFM) basis to test if the expected reduction in h_n^2 for individual plant selection due to microenvironmental variance is present within the NL-94 population.

Estimates of h_n^2 on an individual plant basis were derived as follows:

$$h_n^2 = \frac{4\sigma_F^2}{\sigma_F^2 + \sigma_{FE}^2 + \sigma_{FY}^2 + \sigma_{FEY}^2 + \sigma_\gamma^2 + \sigma_e^2 + \sigma_w^2}$$

Estimates of h_n^2 on a PFM basis where analyses were conducted over environments were calculated as follows:

$$h_n^2 = \frac{\sigma_F^2}{\sigma_F^2 + \sigma_{FE}^2/E + \sigma_{FY}^2/Y + \sigma_{FEY}^2/EY + \sigma_\gamma^2/RE + \sigma_e^2/REY}$$

where σ_F^2 is variance attributable to plant families (genotypes), σ_{FE}^2 is variance attributable to family \times environment interaction, σ_{FY}^2 is variance attributable to family \times year interaction, σ_{FEY}^2 is variance attributable to family \times environment \times year interaction, σ_γ^2 is variance attributable to families \times replications within environments, σ_e^2 is experimental error, mean 0, variance σ^2 , σ_w^2 is variance attributable to individual plants within plots, E is number of environments, Y is number of years, R is number of replications, and N is number of plants per plot.

For analyses of data within a particular environment the genetic variance term corresponding to family \times environment and family \times environment \times year components were omitted from the formulae. The formulae above provide an estimate of h_n^2 because the genetic variance among HS families represents primarily the additive genetic variance contained in the phenotypic variance among HS plot family means and among individual plants (Nguyen & Sleper 1983). A 95% confidence interval (CI) was calculated for each h_n^2 estimate. For all analyses, standard errors of h_n^2 estimates from variance components were obtained via the method described by Nelder (1953) in order to obtain CIs.

ΔG per cycle of selection was calculated on both an individual plant and PFM basis as described by Nguyen and Sleper (1983). ΔG per cycle of individual plant selection can be predicted as follows:

$$\Delta G = ck h_{ph}^2 \sigma_{ph} = ck \frac{4\sigma_F^2}{\sigma_p}$$

ΔG per cycle of selection based on a PFM basis can be estimated as follows:

$$\Delta G = ck h_{pfm}^2 \sigma_{pfm} = ck \frac{\sigma_F^2}{\sigma_{pfm}}$$

where c is parental control factor, k is standardized selection differential, h_{ph}^2 is narrow-sense heritability on an individual plant basis, σ_{ph} is phenotypic standard deviation from individual plant analysis, h_{pfm}^2 is narrow-sense heritability on a PFM basis, σ_{pfm} is phenotypic standard deviation from PFM analysis, σ_F^2 is variance attributable to plant families.

Here, $c = 2$ and $k = 1.16$.

Results and discussion

Yield environment effects on selection

C₀ populations

Mean dry biomass yields of C_0 clonal HS families differed significantly in the HYE and LYE tests as determined by a Student's *t*-test (Table 1). Selections from the NL-94 C_0 population used to form the NL-94 HYE and NL-94 LYE C_1 populations were based upon 1998 mean dry weight biomass yields of HS plant families tested within the HYE and LYE, respectively. Nine of 14 parents were common to the two protocols based on HS progeny testing under HYE and LYE. Selection of C_0 parent plants based on 3-year mean HS yield data would have resulted in slight changes in the array of selected plants.

Table 1 Mean (range) dry biomass yields of 65 NL-94 switchgrass C_0 half-sib families evaluated in low-yield environment (LYE) and high-yield environment (HYE) tests at Stillwater, OK, 1998–2000

Year	LYE (kg plant ⁻¹)	HYE (kg plant ⁻¹)	<i>P</i> -value (two sided)	<i>P</i> -value (one sided)	LSD (0.05) (kg plant ⁻¹)
1998	0.82 (0.27–1.27)	1.22 (0.55–2.02)	<0.0001	<0.0001	0.05
1999	1.76 (0.95–2.59)	3.77 (2.24–5.63)	<0.0001	<0.0001	0.07
2000	0.98 (0.51–2.00)	2.76 (1.78–4.00)	<0.0001	<0.0001	0.05
Over years	1.184 (0.057–1.95)	2.580 (1.62–3.78)	<0.0001	<0.0001	0.02

Eleven and nine of the 14 parent plants selected on the basis of 1998 HS family mean yields would also have been selected based on 3-year mean yields of the HS families in HYE and LYE, respectively. However, based on LSD values of 0.59 and 0.28 for HS families in the HYE and LYE, respectively, only one selection in the HYE and two in the LYE were significantly different for 1998 means vs. the 3-year mean yields. These findings are further supported in that Spearman's rank correlation coefficients of $r_s = 0.83$ in the HYE and $r_s = 0.84$ in the LYE ($P < 0.01$ for both) were obtained when comparing all family ranks for 1998 vs. the 3-year mean yields.

C₁ populations

Mean dry biomass yields of C_1 HS families differed significantly ($P < 0.01$) between the HYE and LYE tests over years and were approximately 2.5 times greater in HYE than LYE (Table 2). Biomass yield differed significantly between selection protocols in each test environment within each year except for the 2004 LYE test (Table 2). Yield differences due to family_(protocol) were significant in all years of the test (data not shown). Mean yields of HS families from the S_{LYE} protocol were consistently greater than those from the S_{HYE} protocol in both the HYE and LYE tests as determined by a Student's *t*-test (Table 2). The environment, year, and environment \times year effects were all highly significant ($P < 0.01$, data not shown).

In order to describe the effects of GE interaction, the ratio of variation attributable to GE interaction to total phenotypic variation was obtained. For the combined analysis over years and locations the GE interaction (family_(protocol) \times environment, family_(protocol) \times year, and family_(protocol) \times environment \times year) comprised 58% of the total phenotypic variation. Hence, the magnitude of GE interaction was substantial and is postulated to be attributable to the high variance component corresponding to family_(protocol) \times environment effect (Table 3). For the analyses conducted within environments, the amount of GE interaction variation (family_(protocol) \times year) to total phenotypic variation was found to be 0% for both the HYE and

Table 2 Mean (range) dry biomass yields of NL-94 LYE and NL-94 HYE switchgrass C_1 half-sib (HS) families tested under a low-yield environment (LYE) and a high-yield environment (HYE) at Stillwater, OK, 2002–2004

Protocol	LYE (kg plant ⁻¹)			HYE (kg plant ⁻¹)			Over years		
	2002	2003	2004	2002	2003	2004	2002	2003	2004
S_{LYE}	1.31 (0.62–2.04)	1.53 (0.95–2.07)	2.17 (1.22–3.25)	4.04 (3.70–4.83)	3.66 (2.80–4.33)	4.46 (2.82–5.79)	4.05 (2.99–4.96)	4.05 (2.99–4.96)	4.05 (2.99–4.96)
S_{HYE}	1.17 (0.68–2.00)	1.43 (0.90–2.05)	2.03 (1.19–2.81)	3.85 (2.62–4.60)	3.50 (2.69–4.55)	4.28 (3.01–5.40)	3.88 (2.80–4.78)	3.88 (2.80–4.78)	3.88 (2.80–4.78)
\bar{x}	1.24 (0.62–2.04)	1.48 (0.90–2.07)	2.10 (1.19–3.25)	3.95 (2.62–4.83)	3.58 (2.69–4.55)	4.37 (2.82–5.79)	3.97 (2.80–4.78)	3.97 (2.80–4.78)	3.97 (2.80–4.78)
<i>P</i> -value (two sided)	0.003	0.027	0.066	0.002	0.012	0.048	<0.0001	<0.0001	<0.0001
<i>P</i> -value (one sided)	0.006	0.054	0.132	0.004	0.024	0.096	0.0002	0.0002	0.0002
LSD (0.05)	0.08	0.08	0.14	0.11	0.11	0.17	0.07	0.07	0.07

Protocols (S_{LYE} and S_{HYE}) consist of 65 and 60 HS C_1 families originating respectively from selection in the C_0 population under LYE and HYE protocols
P-value denotes differences between S_{LYE} and S_{HYE} within and over years

Table 3 Estimates of variance components and their associated standard errors for 125 NL-94 switchgrass half-sib (HS) families evaluated for biomass yield in

high-yield environment (HYE) and low-yield environment (LYE) tests at Stillwater, OK, 2002–2004

Variance component	Test environment		
	HYE	LYE	HYE + LYE
Family/ S_P (σ_F^2)	0.1189 \pm 0.0207**	0.0542 \pm 0.0105**	0.0004 \pm 0.0006
Environment (E) \times family/ P (σ_{FL}^2)	–	–	0.0045 \pm 0.0008**
Year \times family/ P (σ_{FY}^2)	0 \pm 0	0 \pm 0	0 \pm 0
$E \times Y \times$ family/ P (σ_{FLY}^2)	–	–	0 \pm 0
Residual (σ_e^2)	0.5180 \pm 0.0198	0.3283 \pm 0.0125	0.0283 \pm 0.0008

Protocols (P) consist of 60 and 65 families originating respectively from *HYE* and *LYE* C_0 selection protocols

*,** Significant at the 0.05 and 0.01 probability levels, respectively

LYE tests when averaged over years and replications. In Fig. 1, yields from plant families in the LYE were plotted in ascending order of magnitude and yields from plant families in the HYE were plotted relative to corresponding families within the LYE. No crossover-type GE interactions are indicated in Fig. 1.

Plants that would be selected from the HYE and LYE C_1 selection nurseries based on yield performance of the 125 C_1 HS families tested under HYE and LYE is of interest. Based on 3-year mean yields and a 30% selection intensity (40 of 125 plants), 17 of the 40 C_1 parent plants selected from the HYE and LYE C_1 selection nurseries would be in common. Twenty-six and 14

of the 40 plants would trace respectively to the S_{LYE} and S_{HYE} protocols. A Spearman's rank correlation of $r_s = 0.14$ was calculated for HS family biomass yields from the HYE and LYE tests. This low correlation and the high ratio of GE variation to total phenotypic variation are indicative of the differential effects of yield environment on HS family biomass yields.

Estimation of genetic parameters based on C_1 HS progeny

Analysis of data over the yield environments indicated a low estimate (0.0004 ± 0.0006) of the family(protocol) variance component (Table 3). Estimates of h_n^2 and predicted gain from selection based on the combined data of both C_0 protocols (S_{HYE} and S_{LYE}) over HYE and LYE were correspondingly low (Tables 4, 5). Analysis of data within the respective HYE and LYE tests resulted in much higher family(protocol) variance estimates, h_n^2 estimates, and ΔG (Tables 3, 4, 5). The family(protocol) variance for the HYE (0.1189 ± 0.0207) was approximately twice that of the LYE (0.0542 ± 0.0105) (Table 3). Estimated h_n^2 was higher for the HYE (0.73) than for the LYE (0.65) when based on calculations from HS PFM performance (Table 4). These differences are consistent with results for grain yield in crops such as maize (*Z. mays* L.) where genetic variance and h_n^2 have generally been found to decrease when moving from high- to low-yield conditions (Banziger & Cooper 2001). However, Atlin and Frey (1989) found no consistent

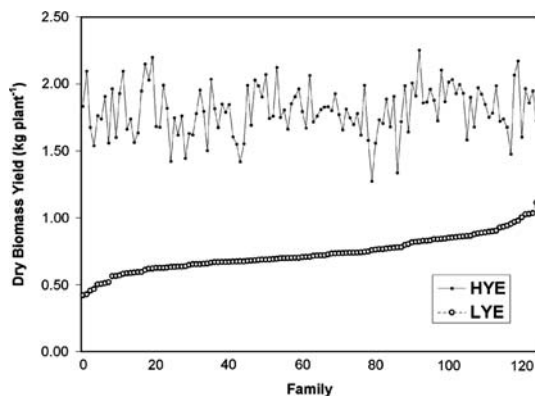


Fig. 1 Graphical representation of 3-year (2002–2004) mean dry biomass yields (kg plant^{-1}) of 125 NL-94 C_1 half-sib families plotted by family for high yield environment (HYE) and low yield environment (LYE) tests. Yields from families in the LYE were plotted in ascending order of magnitude, yields from families in the HYE were plotted relative to corresponding families within the LYE

Table 4 Estimates of narrow-sense heritability (h_n^2) for biomass yield, 95% confidence intervals (CIs) of those h_n^2 estimates, and predicted genetic gains (ΔG) per cycle of selection (5 years per cycle) and per year for the NL-94

Population	h_n^2 estimate	95% CI	ΔG selection cycle (kg dm)	ΔG year (kg dm)
Combined analysis	0.09	(0.03, 0.12)	0.014	0.003
S _{HYE} protocol over environments	0.08	(−0.010, 0.26)	0.012	0.002
S _{LYE} protocol over environments	0.18	(0.12, 0.24)	0.027	0.005
HYE (S _{HYE} + S _{LYE})	0.73	(0.61, 0.85)	0.685	0.137
LYE (S _{HYE} + S _{LYE})	0.65	(0.56, 0.74)	0.434	0.087
S _{HYE} protocol within HYE	0.76	(0.67, 0.88)	0.734	0.148
S _{HYE} protocol within LYE	0.67	(0.65, 0.69)	0.439	0.088
S _{LYE} protocol within HYE	0.70	(0.56, 0.84)	0.634	0.127
S _{LYE} protocol within LYE	0.62	(0.38, 0.86)	0.434	0.086

relationship between heritability and mean yield of the selection environment for oat (*Avena sativa* L.). Presterl et al. (2003) likewise indicated no consistent relationship between heritability and mean yield of the selection environment for European maize (*Z. mays* L.) at several locations in Germany and France. Conversely, the h_n^2 estimates were higher for LYE (HYE = 0.33, LYE = 0.48) when based on individual HS progeny plant performance (Table 5). Estimates of h_n^2 based on selection protocols within the respective HYE and LYE tests were higher for S_{HYE} than for S_{LYE} and consistent with estimates derived over protocols for the HS PFM and individual progeny performance data when tested in single environments (Tables 4, 5). Within HYE and LYE test environments, ΔG in dry biomass yield ranged from 0.349 to 0.734 kg plant^{−1} cycle^{−1} (Tables 4, 5). The highest estimate of ΔG

high-yield environment (HYE) and low-yield environment (LYE) C₁ populations based on calculations from variance components using phenotypic family means

(0.734) was obtained from selection based on the S_{HYE} protocol within the HYE for PFM. Discounting selection protocols (S_{HYE} and S_{LYE}), estimates of ΔG based on HS PFM performance was higher for HYE (0.685 kg plant^{−1} cycle^{−1}) compared to LYE (0.434 kg plant^{−1} cycle^{−1}) (Table 4). When based on individual HS progeny plants, estimates of ΔG were 0.403 and 0.392 kg plant^{−1} cycle^{−1} for the HYE and LYE, respectively (Table 5). This is consistent with studies that have shown that ΔG is lower under low-input environments (Brancourt-Hulmel et al. 2005). All h_n^2 estimates were higher when based on HS PFM performance compared to individual HS progeny performance. For analyses conducted per C₀ protocol and over environments for PFM selection, h_n^2 estimates were 0.08 and 0.18 for S_{HYE} and S_{LYE}, respectively. Corresponding estimates of ΔG from this PFM selection method

Table 5 Estimates of narrow-sense heritability (h_n^2) for biomass yield, 95% confidence intervals (CIs) of those h_n^2 estimates, and predicted genetic gains (ΔG) per cycle of selection (5 years per cycle) and per year for the NL-94

Population	h_n^2 estimate	95% CI	ΔG selection cycle (kg dm)	ΔG year (kg dm)
Combined analysis	0.03	(−0.02, 0.04)	0.015	0.003
S _{HYE} protocol over environments	0.02	(−0.15, 0.19)	0.011	0.002
S _{LYE} protocol over environments	0.03	(0.01, 0.05)	0.018	0.004
HYE (S _{HYE} + S _{LYE})	0.33	(0.24, 0.42)	0.403	0.081
LYE (S _{HYE} + S _{LYE})	0.48	(0.30, 0.66)	0.392	0.078
S _{HYE} protocol within HYE	0.39	(0.27, 0.51)	0.464	0.093
S _{HYE} protocol within LYE	0.50	(0.40, 0.60)	0.393	0.079
S _{LYE} protocol within HYE	0.28	(0.11, 0.45)	0.349	0.070
S _{LYE} protocol within LYE	0.47	(0.19, 0.75)	0.391	0.078

high-yield environment (HYE) and low-yield environment (LYE) C₁ populations based on calculations for individual plant selection

were 0.012 and 0.027 kg plant⁻¹ cycle⁻¹ for S_{HYE} and S_{LYE}, respectively. Discounting protocols, the within environment ΔG was higher for PFM.

Conclusions

Testing of HS progeny plants for one vs. three post-establishment years would result in a high percentage of the same plants being selected as indicated by significant Spearman's rank correlations of $r = 0.83$ and $r = 0.84$ for LYE and HYE C₀ HS performance tests, respectively. The relatively high estimates of variance attributable to families and ΔG indicated a high potential for increasing dry biomass yields via RSGCA in the NL-94 switchgrass population. Selection based on PFM compared to individual plant selection resulted in higher estimates of h_n^2 and ΔG within the HYE. For individual plant selection, the h_n^2 estimate was higher for LYE compared to HYE, but ΔG were similar. It is postulated that greater variance attributable to the microenvironment and to replications within the HYE is responsible for this phenomenon. The results suggest that the biomass yield environment in which HS families are evaluated influences plant selection to a moderate degree. Mean dry biomass yields of C₁ HS families from selection under the S_{LYE} protocol were consistently higher than those from C₁ HS families originating from selection under the S_{HYE} protocol in both HYE and LYE, suggesting that selection under LYE conditions in the C₀ population would produce more favorable yield gains within C₁ populations. The estimates of h_n^2 and ΔG from the C₁ populations indicate that positive response to selection for biomass yield is possible in subsequent cycles of selection under either HYE or LYE, with the advantage trending to HYE.

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